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Digestively constrained predators evade the cost of interference competition

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Summary

1. Models of functional and aggregative responses generally assume that rates of prey encounter and handling times limit a predator's intake rate (Holling's disc equation). Two different lines of approach build upon this fundamental foraging concept. In the first, mutual interference further constrains intake rate, while in the second, intake rate may be constrained by rate of digestion. By combining both approaches, we come up with four competing models that differ in whether predators interfere and whether they face a digestive constraint.

2. The functional responses expected by these four models are tested experimentally in a medium-sized shorebird, the red knot (*Calidris canutus*), fed a shelled prey, the blue mussel (*Mytilus edulis*). The experimental results suggest that intake rate is constrained by rate of digestion at low bird densities and by interference at high bird densities.

3. Using the experimentally obtained parameters, we predicted aggregative responses for each of the four models, which we verified by using field observations. We found evidence that the combination of interference and digestive constraints similarly governed the aggregative responses of red knots. Compared to the expectations of the models that do not include digestive constraints, red knots fed in lower and more variable prey densities and were generally aggregated in denser flocks. In addition, they were packed twice as densely when feeding on hard-shelled prey than when feeding on soft-bodied prey.

4. We suggest that digestive constraints allow red knots to live in dense flocks: if digestion proceeds during interference interactions, the time-cost of interference may be negligible.

Key-words: aggregative response, *Calidris canutus*, digestive constraint, functional response, interference competition.

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Introduction

The response of predators to prey density is important in the dynamics of communities (Fryxell & Lundberg 1997). It comprises two parts: (1) the functional response: a predator's intake rate in relation to prey density, and (2) the aggregative response: how predators distribute themselves across patches with different prey densities. As intake rates usually increase with increasing prey densities, aggregative responses of predators aiming to maximize their long-term average intake rates (Stephens & Krebs 1986) are straightforward: all predators should gather in the patch that contains the highest prey density (assuming that moving between patches incurs at no cost). Usually, predators occupy more than simply the richest patch, which is generally related to interference competition (Bautista, Alonso & Alonso 1995), energetic costs of moving between patches (Bernstein, Kacelnik & Krebs 1991), non-energetic costs of foraging (Brown 1988) or to imperfect information about resource densities (Piersma *et al*. 1995). The topic of this paper will be the role of interference competition, defined as the decline in intake rate due to the presence of competitors (Goss-Custard 1980). Such interference happens either (1) through time loss to interactions with competitors, or (2) through an increase in search time because prey respond adaptively to the presence of predators by making themselves harder to find ('prey depression', e.g. Yates, Stillman & Goss-Custard 2000). Here we focus on the first form of interference, which has

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received by far the most attention, and forms the basis of much current thinking about aggregative responses (Tregenza 1995; van der Meer & Ens 1997; Abrams & Ginzburg 2000; Skalski & Gilliam 2001; Vucetich, Peterson & Schaefer 2002).

Most conceptual models of 'interaction interference' are built upon the interference-free Holling's disc equation (Holling 1959; see Jeschke, Kopp & Tollrian 2002 for review). In this fundamental functional response model, intake rate is so-called 'handling-limited' (*sensu* Farnsworth & Illius 1998; Jeschke *et al*. 2002), meaning that the maximum long-term intake rate is constrained by the rate at which prey can be handled externally (the asymptote in Holling's disc equation). Similarly, most models of interference also consider intake rate to be 'handling-limited'. However, as suggested recently by Jeschke *et al*. (2002), most predators are 'digestion-limited' rather than 'handling-limited', meaning that their maximum long-term rates of intake are constrained by digestion rate.

In this paper we consider four functional response models: a 'handling-limited' and a 'digestion-limited' model, both with and without interference. These models are tested experimentally in captive red knots (*Calidris canutus* L.), medium-sized shorebirds that make a living by foraging in dense flocks on intertidal mudflats (Zwarts & Blomert 1992; Piersma *et al*. 1993) and may often be 'digestion-limited' due to their habit of ingesting large amounts of bulky shell material (van Gils *et al*. 2003a,b). Extrapolation of the experimental results allowed us to predict four unique aggregative responses, which are examined with observational data on free-living red knots.

FOUR FUNCTIONAL RESPONSE MODELS

(1) Interference-free, handling-limited

The most simple and fundamental functional response model is Holling's disc equation (Holling 1959), in which neither interference nor digestion is considered. Foraging comprises only searching and handling prey. In an area containing X randomly distributed prey items, the intake rate *while foraging*, called short-term intake rate (cf. Fortin, Fryxell & Pilote 2002), is therefore given by:

$$IR_{short\text{-}term} = \frac{aX}{1 + ahX} \qquad \text{eqn 1}$$

where h is handling time (s) and a is searching efficiency (fraction of the area effectively searched/s; Hassell 1982). Because predators in this model spend all their time foraging, this equation also gives their long-term average intake rate (calculated over total time; *sensu* Fortin *et al*. 2002; Fig. 1), or formally:

$$IR_{long\text{-}term} = IR_{short\text{-}term} \qquad \text{eqn 2}$$

We will refer to this model as model 1.

(2) Interference- and handling-limited

In conceptual interference models, foraging predators spend time not only searching and handling, but also interfering in order to gain space or prey from competitors. Such models come in two categories, depending on how predators respond to encounters with competitors: either they respond (i) in a fixed way (e.g. Beddington 1975; DeAngelis, Goldstein & O'Neill 1975; Crowley & Martin 1989; Ruxton, Guerney & de Roos 1992) or (ii) in an optimal way (which depends on the difference in social dominance, e.g. Stillman, Goss-Custard & Caldow 1997; Broom & Ruxton 1998; Sirot 2000). For reasons of mathematical tractability, we focus on the former category of interference models. Within this category, the models only differ in whether, and how, handling predators are involved in interference interactions. These models therefore make different predictions for foragers with relatively long handling times such as oystercatchers (*Haematopus ostralegus*; van der Meer & Ens 1997), but not for foragers with relatively short handling times, such as red knots (Zwarts & Wanink 1993; Piersma *et al*. 1995). We therefore selected the most direct derivative of Holling's disc equation as formulated by Crowley & Martin (1989; but we could have equally taken the model by Beddington 1975; DeAngelis *et al*. 1975; or Ruxton *et al*. 1992). In this model, both searching and handling predators can potentially initiate interactions with both searching and handling predators (which has been observed in foraging red knots, personal observation). In this case, intake rate while foraging (which now comprises searching, handling and interfering) is given by:

$$IR_{short\text{-}term} = \frac{aX}{1 + ahX + q(P-1)(1 + ahX)} \qquad \text{eqn 3}$$

where q is a measure of the strength of interference, the so-called interference area (fraction of total patch size; see van der Meer & Ens 1997 for the subtle difference between the mechanistic q and the better-known, phenomenological interference coefficient m as introduced by Hassell & Varley 1969), and P is the total number of predators in the patch (≥ 1). $IR_{short\text{-}term}$ equals Holling's interference-free intake rate at $P = 1$ and declines with increasing values of P (Fig. 1). For any value of X but for a given value of P, $IR_{short\text{-}term}$ is a constant proportion $(1/(1 + q(P-1)))$ of Holling's interference-free intake rate (eqn 1), which is why we rated this model to be the most direct derivative of the disc equation (in other interference models this proportion varies with P and X). Because predators in this model spend all their time foraging, the following condition holds (Fig. 1):

$$IR_{long\text{-}term} = IR_{short\text{-}term} \qquad \text{eqn 4}$$

We will refer to this model as model 2.

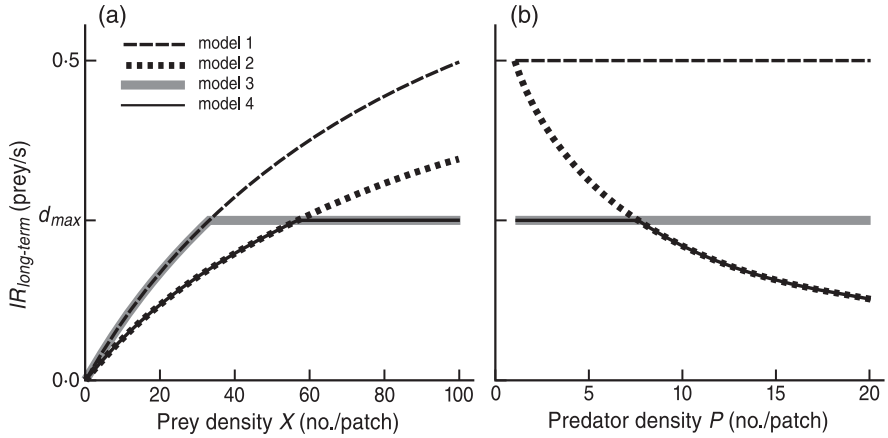

Fig. 1. Four functional response models that predict long-term intake rate ($IR_{long\text{-}term}$) as a function of (a) prey density X and (b) predator density P (in (a): $P = 4$; in (b): $X = 100$). In Holling's disc equation (model 1; dashed line), $IR_{long\text{-}term}$ is constrained only by rate of prey encounter (which increases with prey density) and rate of handling (the asymptote of the curve). In model 2 (dots), $IR_{long\text{-}term}$ is constrained additionally by rate of interference and therefore declines with increasing predator density. In addition to constraints set by rate of prey encounter and rate of handling, $IR_{long\text{-}term}$ in model 3 (grey line) is constrained by the rate at which prey can be digested and is therefore truncated at the maximum rate of digestion (d_{max}). Compared to model 3, $IR_{long\text{-}term}$ in model 4 (solid line) is additionally constrained by rate of interference.

(3) Interference-free, digestion-limited

Digestion is assumed to be unaffected by behaviour, i.e. it proceeds at a constant rate in the 'background' of other activities, be it searching, handling or any other activity (Jeschke *et al*. 2002). As long as the rate of digestion can keep up with $IR_{short\text{-}term}$ (given by eqn 1 for this model), $IR_{long\text{-}term}$ is 'handling-limited' and equals $IR_{short\text{-}term}$ (Fig. 1). However, $IR_{long\text{-}term}$ becomes 'digestion-limited' whenever $IR_{short\text{-}term}$ exceeds the maximum rate of digestion (which is set by digestive organ size; van Gils *et al*. 2003a; see also Kirkwood 1983; Kvist & Lindström 2003; Karasov & McWilliams 2004). In order to free some space in its filled gastrointestinal tract, a 'digestion-limited' predator needs to continue digestion at full speed, but slow down or stop foraging (digestive breaks), such that $IR_{long\text{-}term}$ (which is calculated over total time and thus includes digestive breaks) equals the maximum rate of digestion (McNamara & Houston 1997; van Gils *et al*. 2003b). Thus, $IR_{long\text{-}term}$ (prey/s) simply equals whichever process is slowest, $IR_{short\text{-}term}$ (prey/s) or the maximum rate of digestion d_{max} (prey/s; Fig. 1), or formally:

$$IR_{long\text{-}term} = \min(IR_{short\text{-}term}, d_{max}) \qquad \text{eqn 5}$$

Restricted to herbivores, this model has been formulated earlier by Fryxell (1991), Wilmshurst, Fryxell & Colucci (1999), Wilmshurst, Fryxell & Bergman (2000) and Owen-Smith (2002). More complex models, where predators respond to the degree of gut fullness, are treated by Holling (1966), Metz & van Batenburg (1985a, 1985b), Sabelis (1986) and Metz, Sabelis & Kuchlein (1988). Applying eqn 5 to digestively constrained red knots living in an interference-free environment predicted successfully (i) $IR_{long\text{-}term}$, and (ii) the amount of time lost to digestive breaks (van Gils *et al*. 2003b). We will refer to this model as model 3.

(4) Interference- and digestion-limited

The model is structurally similar to model 3, and thus (Fig. 1):

$$IR_{long\text{-}term} = \min(IR_{short\text{-}term}, d_{max}) \qquad \text{eqn 6}$$

where $IR_{short\text{-}term}$ is now given by eqn 3. We will refer to this model as model 4.

FROM FUNCTIONAL RESPONSES TO AGGREGATIVE RESPONSES

In an environment consisting of patches that contain different prey densities, aggregative response equations can be used to predict how predators distribute themselves across these patches. To establish such equations, it is generally assumed that (i) movements between patches incur at no cost, and that all predators are (ii) identical, (iii) omniscient and (iv) aim to maximize $IR_{long\text{-}term}$. The latter point is a core assumption in optimal foraging theory (Stephens & Krebs 1986). Although some recent studies showed maximization of short-term intake rate, explained by fitness-costs associated with foraging (Illius *et al*. 1999; Bergman *et al*. 2001; Fortin *et al*. 2002), maximization of long-term intake rate seems to be the general 'rule' (reviewed by Stephens & Krebs 1986; Maurer 1996; Sih & Christensen 2001), notably also in red knots (van Gils *et al*. 2003b). Given these conditions, predators will distribute themselves according to the 'ideal free distribution' (IFD; Fretwell & Lucas 1970), which implies that they cannot increase their intake rate by moving to other another patch. This maximal $IR_{long\text{-}term}$ in an IFD is defined as c (prey/s).

(1) Interference-free, handling-limited

Because $IR_{long\text{-}term}$ is a simple, positive function of prey density and is unaffected by predator density (eqn 1 via eqn 2), it is maximal in the patch containing the highest prey density (defined as X_{max}) which is where, according to this model, all predators should gather. Formally,

$$P \geq 1 \quad \text{for} \quad X = X_{max} \qquad \text{eqn 7a}$$

$$P = 0 \quad \text{for} \quad X < X_{max} \qquad \text{eqn 7b}$$

(2) Interference- and handling-limited

In contrast to the previous model, where the value of c simply equals $IR_{long\text{-}term}$ at X_{max}, the value of c in this model depends on the total number of predators in the environment and on the frequency distribution of patches in terms of prey density and surface area (see van der Meer & Ens 1997 for derivation). In any case, it lies between zero and $< 1/h$, which is the maximum interference-free intake rate. Once derived, it should be equated to the functional response (eqn 3 via eqn 4):

$$\frac{aX}{1 + ahX + q(P-1)(1+ahX)} = c \qquad \text{eqn 8}$$

Solving this equation for P gives the expected aggregative response:

$$P = -\frac{1}{q} + \frac{aX}{cq(1+ahX)} + 1 \qquad \text{eqn 9}$$

Thus, according to this model, predators gather in different patches where their density P is a unique and positive function of prey density X. Note that for patches with $X < 1/(a(1/c - h))$ predator density P becomes < 1 and should be set to zero; formally:

$$1 \leq P \leq -\frac{1}{q} + \frac{aX}{cq(1+ahX)} + 1 \text{ for } X \geq \frac{1}{a(1/c - h)} \qquad \text{eqn 10a}$$

$$P = 0 \text{ for } X < \frac{1}{a(1/c - h)} \qquad \text{eqn 10b}$$

(3) Interference-free, digestion-limited

Because $IR_{long\text{-}term}$ cannot exceed the maximum digestive rate d_{max} (eqn 5), the maximum possible intake rate c throughout the environment is achieved in patches where $IR_{short\text{-}term}$ (defined in eqn 1) at least equals d_{max}:

$$\frac{aX}{1+ahX} \geq d_{max} = c \qquad \text{eqn 11}$$

Solving for X shows that these are patches where

$$X \geq \frac{1}{a(1/d_{max} - h)} \qquad \text{eqn 12}$$

Thus, according to this model, as long as patches contain a minimal number of prey (defined by eqn 12), predators should distribute themselves in those patches, irrespective of the number of prey that they harbour or the number of predators already present (there is no interference). Formally,

$$P \geq 1 \quad \text{for} \quad X \geq \frac{1}{a(1/d_{max} - h)} \qquad \text{eqn 13a}$$

$$P = 0 \quad \text{for} \quad X < \frac{1}{a(1/d_{max} - h)} \qquad \text{eqn 13b}$$

(4) Interference- and digestion-limited

Because $IR_{long\text{-}term}$ cannot exceed the maximum digestive rate d_{max} (eqn 6), the maximum possible intake rate c throughout the environment is achieved in patches where $IR_{short\text{-}term}$ (defined in eqn 3) at least equals d_{max}:

$$\frac{aX}{1 + ahX + q(P-1)(1+ahX)} \geq d_{max} = c \qquad \text{eqn 14}$$

Solving for P shows that in these patches

$$P \leq -\frac{1}{q} + \frac{aX}{d_{max}q(1+ahX)} + 1 \qquad \text{eqn 15}$$

In this equation, predator densities < 1 should be set to zero, thus:

$$1 \leq P \leq -\frac{1}{q} + \frac{aX}{d_{max}q(1+ahX)} + 1 \qquad \text{eqn 16a}$$

$$\text{for } X \geq \frac{1}{a(1/d_{max} - h)}$$

$$P = 0 \text{ for } X < \frac{1}{a(1/d_{max} - h)} \qquad \text{eqn 16b}$$

Thus, according to this model, within certain lower limits on prey densities and upper limits on predator densities (eqn 16a), predators should distribute themselves across patches, irrespective of the number of prey that they harbour or the number of predators already present.

OBJECTIVES AND APPROACH

In this paper we test how and whether interference and rate of digestion constrain a predator's $IR_{long\text{-}term}$. As model predators we have chosen red knots. As most of their prey comprises bulky, indigestible shell material, the gastrointestinal tract of red knots fills quickly after feeding commences (depending on prey size, usually after three to nine prey ingestions). Thus, red knots

face a digestive constraint at relatively low (short-term) intake rates and regularly need to take digestive breaks (lasting 20–300 s; Zwarts & Blomert 1992; van Gils *et al*. 2003a,b). When eating bivalve prey whose shell was removed experimentally, $IR_{long\text{-}term}$ increased by 100–400% (van Gils *et al*. 2003a). This suggests strongly that it is the bulky shell material that constrains a red knot's intake digestively over total time.

Red knots live in flocks of up to 10 000 individuals (Piersma *et al*. 1993). These flocks are dense and the likelihood of interference competition would seem high. At the same time, however, the very fact that these birds allow close proximity suggests that the cost of interference competition is low relative to the benefits of living in a flock (antipredation, information). How strong is interference in red knots and what are the consequences of interference for long-term intake rate?

An experiment was set up to answer these questions, in which we tested which of the four conceptual functional response models best predicted $IR_{long\text{-}term}$ at different flock sizes. We then proceeded to see which of these models best predicted aggregative responses as observed in the field.

Material and methods

EXPERIMENT: THE PREDATORS, THEIR HOUSING AND THEIR PREY

The experiment was carried out from 25 to 30 June 2000 with five adult red knots. These birds were captured in the western Dutch Wadden Sea (53°15′ N, 5°15′ E) in 1994–99. To accustom them to the experimental setting, 1 week before the experiment started the birds were moved from their permanent outdoor aviaries to the indoor experimental arena. Here they lived in a stable environment with respect to light (L : D = 15 : 9) and temperature (18 °C), in a small aviary measuring 4 × 1 m surface × 3 m high. The experiment took place in a basin in a larger aviary (7 × 7 m surface × 3 m high) just next to the small aviary. The basin was filled with 30-cm-deep seawater. The experimental patch, a small tray (0·25 m^2 × 30 cm high), was placed in the middle of the basin, elevated slightly above the water level, such that it mimicked a natural exposed patch of mud. The patch was filled with sediment collected in the western Dutch Wadden Sea (Mokbaai, Texel). Before the start of each trial, we washed out the sediment to make sure no prey items remained from the previous trial. After replacing the washed sediment, we inserted the prey items in the sediment at a fixed depth of 2 cm at random positions (see Piersma *et al*. 1995). The birds that were not participating in a trial were put into a small box for as long as the trial lasted. Once we opened the door to the large experimental room, the birds that remained in the small aviary would fly immediately to the patch. This defined the start of a trial. We closed the door of the small aviary in order to keep all selected birds on the patch during the trial. This door was opened again at the end of a trial. A Hi-8 video camera placed at a distance of 1·5 m from the patch recorded each trial. Zoom was kept constant and selected such that all flock members were always in view. Tapes were analysed with the software package The Observer (Noldus Information Technology 1997). This allowed us to play back the tapes in slow motion and score, for each flock member, the total number of prey ingested and how long it took each bird to find (either probing or pecking) and handle each prey item (to the nearest 0·04 s). As we kept track of the foraging success of all flock members, we were able to keep track of current prey density, i.e. the initial prey density minus the number of prey captured. In this way, we could separate interference competition from exploitative competition (see below).

Trials were carried out in the afternoon; the birds had access to *ad libitum* staple food during the night. In order to motivate the birds during the trials, food was taken away around 0900 h. At this time, each bird was weighed to the nearest gram. This enabled us to adjust the daily amount of staple food on offer in order to avoid starvation but to keep them lean and eager to feed.

As prey items we used the blue mussel (*M. edulis*). Although mussels usually are attached to rocks, on several occasions we observed red knots feeding upon mussels that were living buried in soft sediments. This justifies the fact that we offered these prey buried during the experiment. We collected the mussels by scraping them from basalt piers in the North Sea at Texel. After washing off most of the attached organic material, we sorted the mussels into different size classes by sieving through different mesh sizes. For the experiment we used the medium size class (mean length ± SEM = 10·9 ± 0·2 mm, mean flesh ash-free dry mass = 10·5 mg, mean shell dry mass = 71·8 mg, n = 49); the other size classes were offered as staple food. Before use, the mussels were stored in basins containing well-aerated seawater of 5–12 °C for a maximum of three weeks.

EXPERIMENT: DESIGN

Flock size on the patch was the experimental treatment, which was comprised of either one bird (n = 5), two birds (n = 6), three birds (n = 4), four birds (n = 5) or five birds (n = 6). To avoid pseudo-replication, each individual was only used once in the one-bird treatment. Individuals were assigned randomly to the two, three- and four-bird treatments. We treated trials as our experimental units, which meant that each trial yielded one value on searching efficiency, handling time and the total number of prey ingested (from which we calculated $IR_{long\text{-}term}$). In each trial, the patch initially contained 20 prey items. We selected this number of prey items to mimic naturally occurring prey densities (cf. Piersma *et al*. 1993). Flock size and composition were assigned randomly to the trials. Each trial lasted 225 s.

PARAMETER ESTIMATES

To model $IR_{long\text{-}term}$ of group-foraging red knots, we needed estimates for searching efficiency (a), handling time (h), maximum digestion rate (d_{max}; required only for models 3 and 4) and interference area (q; required only for models 2 and 4). The estimates for the first three parameters should be interference-free (any effect of interference is mediated by q), and we therefore derived a, h and d_{max} from trials with solitary-feeding birds (a and h from the present 'competition' experiment, while d_{max} was taken from a different 'digestive' experiment – see below). Interference area (q) was derived from all 'competition' trials.

Searching efficiency

Searching efficiency a is defined as the reciprocal of the product of search time between two prey encounters (T_s) and prey density (X). Assuming predators search through their patches randomly, X refers to current prey density (initial prey density corrected for the total number of prey already captured, e.g. Olsson, Brown & Smith 2001):

$$a = \frac{1}{T_s X} \qquad \text{eqn 17}$$

We tested the assumption of random search by testing whether T_s was inversely related to X, i.e. whether these variables were related with a slope of −1 when log-transformed.

As the patch was never emptied during the 225 s that each trial lasted, we included the (unsuccessful) search interval between the last prey encountered and the end of the trial to avoid overestimation of searching efficiency. Such truncated observations are called censored observations, and data sets that contain such observations can be analysed readily by means of survival analysis (Haccou & Meelis 1992). As survival analyses consider lengths of time intervals, we analysed the reciprocals of searching efficiencies, i.e. $T_s X$ (cf. Marschall, Chesson & Stein 1989), using the SURVIVAL module in SYSTAT 10 (Systat Software Inc.). Together with 49 uncensored observations on encountered prey, our data set on searching efficiency comprised 54 observations. As model parameter we used the back-transformed $\log_{10}(a)$ averaged across individuals [applying bias-correction, i.e. antilog(estimate + 2·303 × variance/2)].

Handling time

Handling time h is defined as the time from encountering a prey item, lifting it out of the sediment, positioning it in the bill and ingesting it. We $\log_{10}$-transformed handling times to obtain normal distributions. In total, 49 prey were handled in the five trials with solitary birds. As model parameter we used the back-transformed $\log_{10}(h)$ averaged across individuals (applying bias-correction).

Maximum digestion rate

The upper limit to intake rate due to digestive constraint d_{max} was determined in another experiment specifically designed to measure maximum digestion rates (see van Gils *et al*. 2003a for methodological details). In this 'digestive' experiment, solitary red knots fed on the same prey type as we used here: medium-sized blue mussels of 11·0 mm (SEM = 0·1 mm, n = 149). Prey items were offered unburied and in dense, excess quantities to assure that intake rate was not constrained by search time but by digestive processing rate. As d_{max} is a function the size of the muscular gizzard (van Gils *et al*. 2003a), we made sure that average gizzard mass (± SEM) in the current 'interference' experiment (4·3 ± 0·4 g) was comparable (P = 0·24) with that in the 'digestive' experiment (4·9 ± 0·4 g). Gizzard mass within individual birds was estimated using ultrasonography (Dietz *et al*. 1999), and was 'adjusted' to the aimed size by varying the 'bulkiness' of the staple diet (cf. Dekinga *et al*. 2001). For reasons of methodological consistency with the 'interference' experiment, we estimated d_{max} over the first 225 s of each trial. We defined d_{max} as the average interval between two subsequent prey ingestions (inclusive the last censored interval in each trial). We pooled the data across the two trials per individual bird. Unfortunately, bird D did not participate in this experiment, and an estimate for d_{max} is therefore not available for this individual. As model parameter we used the back-transformed $\log_{10}(d_{max})$ averaged across individuals (applying bias-correction).

Interference area

Parameter q was estimated by fitting eqn 4 (model 2) or eqn 6 (model 4) through observed $IR_{long\text{-}term}$ (while parameterizing these equations with the obtained estimates for a, h and, in case of eqn 6, d_{max}). Because the experiment took place in small, rapidly depleting patches, we had to rewrite the underlying equation for $IR_{short\text{-}term}$ (eqn 3), which holds only for non-depleting prey densities (see Appendix).

FIELD MEASUREMENTS

From 1988 through 1998 (July–November), we estimated predator density in 355 flocks of red knot that fed on mudflats in the western Dutch Wadden Sea, mainly (94%) near the island of Griend (53°15′ N, 5°15′ E). These estimates are based on the spacing of knots within flocks (cf. Stillman *et al*. 2002a). Once a flock was encountered in the distance, we approached it up to 60–100 m and observed the flock by telescope. Neighbour distance D (in units of bird length) is defined as the distance between two neighbouring birds which were standing on a line that was perpendicular to the observer, i.e. angle $\alpha = 90°$. If, unintentionally, this line was not perpendicular (i.e. $\alpha < 90°$), the relative error in D, i.e. (true D)/(estimated D), would be 1/

sin(α). For example, true D would be 5% larger than estimated D if α = 72°. D was estimated for about 5–10 pairs of birds to come to an average neighbour distance D for each flock. This average was transformed into bird density (P, in no./m^2) by making two assumptions: (1) within a flock, individual birds are spaced regularly and (2) bird lengths measure 0·2 m. This led to the following transformation:

$$P = \left(\frac{1}{0{\cdot}2\bar{D}}\right)^2 \qquad \text{eqn 18}$$

Each year (again July–November), we measured prey densities in linear transects (1988–92) or in a regularly spaced grid (1993–98). In the transects, stations were 500 m apart and 20 samples were taken at each station. In the grid, stations were 250 m apart and only one sample was taken at each station (see also Piersma *et al*. 2001). Each sample consisted of sediment taken down to 20 cm with a core of 1/56 m^2. The top (0–4 cm) and bottom (4–20 cm) layers were separated and sieved over 1-mm mesh. In the laboratory, prey items were identified and their lengths were measured to the nearest mm (see Piersma *et al*. 1993, 2001 for further details about prey sampling).

To establish aggregative responses, we linked these prey densities to predator densities by selecting the nearest 20 prey density samples to each observed flock. For the transect data set this meant that all samples came from the same station, for the grid data set this meant that each sample came from a different station. Across these 20 samples, we calculated the available prey density (Piersma *et al*. 1993). This included the accessible (living in the upper four cm of the sediment) and ingestible (up to 15–60 mm in length, depending on species) fraction of 10 bivalve species (so-called hard-shelled prey) and three crustacean species (so-called soft-bodied prey). Two bivalve species dominated these samples, *Macoma balthica* (84%) and *Cerastoderma edule* (10%).

TESTING AGGREGATIVE RESPONSES AGAINST THEORETICAL PREDICTIONS

For each model, we predicted aggregative responses of free-living red knots. For this purpose, we expressed prey and predator densities in units of no./m^2 instead of no./patch as used before. Similarly, we expressed a and q in units of, respectively, m^2/s and m^2, and replaced P by P + 1 in all relevant aggregative response equations (eqns 9, 10a, 15, 16a; see also Skalski & Gilliam 2001). Subsequently, we parameterized these equations by the experimentally obtained estimates on a, h, d_{max} and q. This somewhat simplistic approach of applying the same parameter values across all (available) prey species and sizes is justified by the fact that almost all sampled prey items (94%) belonged to only two prey species that were shown not to differ in a, h (Piersma *et al*. 1995) and d_{max} (van Gils *et al*. 2003a). In addition, although h increases steeply with prey size (Piersma *et al*. 1995), prey densities were usually that low that the effect of h on aggregative responses is negligible (i.e. search times are much longer than handling times). Whether q varies with prey species and size is yet unknown. To obtain a value for c in model 2, we assumed a total of 50 000 red knots occupying our study area (Piersma *et al*. 1993; Bijlsma, Husting & Camphuysen 2001).

Table 1. Analyses and estimates of functional response parameters of solitary-feeding birds. First column gives bird identity, second column gives significance of the slope in $\log_{10}(T_s)$ vs. $\log_{10}(X)$ deviating from –1, third column gives estimates of searching efficiency a (cm^2 s^{-1}), fourth column gives estimates of handling time h (s) and last column gives estimates of maximum digestion rate d_{max} (prey s^{-1})

Bird identity	P-value	a (cm^2 s^{-1})	h (s)	d_{max} (prey s^{-1})
A	0·071	30·9	0·96	0·034
B	0·464	33·1	0·35	0·026
C	0·948	39·4	0·51	0·076
D	0·191	13·3	0·51	–
E	0·078	22·9	0·71	0·017

Results

PARAMETER ESTIMATES

Searching efficiency

None of the five slopes in the relation between $\log_{10}(T_s)$ and $\log_{10}(X)$ deviated from –1 (Table 1), which supports our assumption of random search and allowed us to analyse searching efficiencies in the way we proposed (eqn 17). This led to an average searching efficiency of 26·15 cm^2/s (equals $10{\cdot}5 \times 10^{-3}$ patch size/s) averaged across birds (estimates per individual given in Table 1 and Fig. 2a).

Handling time

The mean handling time across individuals was 0·58 s (Table 1 and Fig. 2b).

Maximal digestion rate

The mean maximal digestion rate across individuals was 0·033 prey/s (Table 1 and Fig. 2c).

Interference area

Fitting model 2 through the observed $IR_{long\text{-}term}$ yielded a q of 0·56 m^2 (or 2·2 when expressed as a multiple of patch size; RSS = 637·8; Fig. 3). In the case of model 4, q was estimated at 0·47 m^2 (1·9 patch size; RSS = 65·4; Fig. 3).

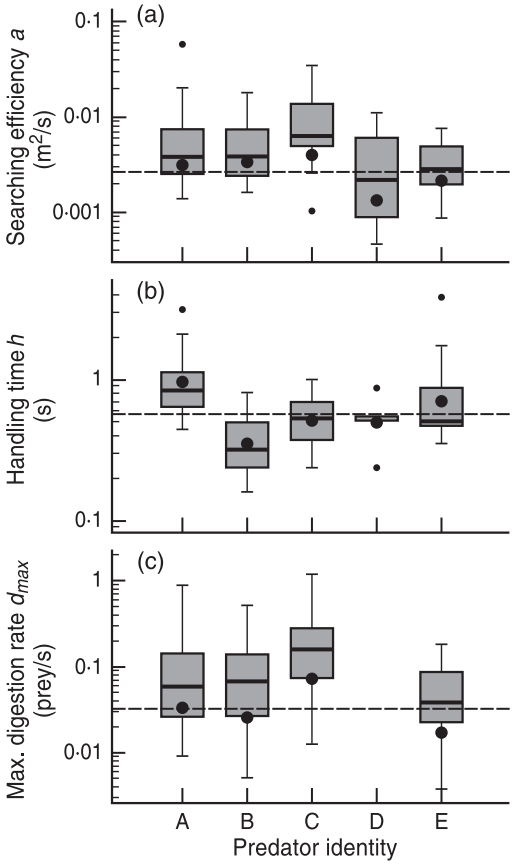

Fig. 2. Three basic functional response parameters collected per solitary-feeding bird. (a) Searching efficiency a, calculated over the search time between two subsequent prey encounters (including censored data). (b) Handling time h per encountered prey. (c) Maximum digestion rate d_{max}, estimated as the reciprocal of the time interval between subsequent ingestions in the 'digestive experiment' (including censored data). In each of the three graphs the horizontal dashed line denotes the average value across individuals. These box-and-whisker plots give mean (large filled dot), median (horizontal line within box), interquartile range (box), range (bars), and outliers (small filled dots).

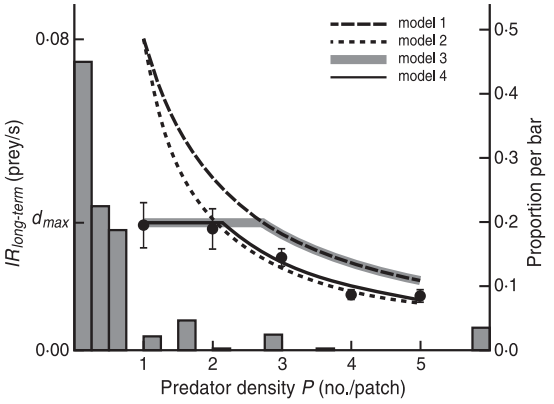

Fig. 3. Long-term intake rate $IR_{long\text{-}term}$ (calculated over the full length of a trial; mean ± SEM scaled on left axis) as a function of the number of predators P in the experimental patch (scaled on lower axis). Based on the functional response parameters obtained on solitary-feeding birds (a, h and d_{max}), $IR_{long\text{-}term}$ is predicted by each model (or fitted with respect to q in the case of models 2 and 4, see main text) and is given by dashed line (model 1), dotted line (model 2), grey line (model 3) or solid line (model 4). Note that these predictions, which take prey depletion into account (see Appendix), differ qualitatively from those outlined in Fig. 1b, which hold for non-depleting scenarios. To compare these results with natural circumstances, we plotted the frequency distribution (scaled on right axis) of red knot densities found in the field. Most densities are such that $IR_{long\text{-}term}$ is constrained by maximum rate of digestion (d_{max}), while only a few are such that $IR_{long\text{-}term}$ is constrained by interference (and exploitative) competition.

LONG-TERM INTAKE RATE AS A FUNCTION OF FLOCK SIZE

Long-term intake rates declined with the number of birds on the patch ($n = 26$, $R^2 = 0{\cdot}53$, $P < 0{\cdot}001$; Fig. 3). Model 1 overestimated $IR_{long\text{-}term}$ across all flock sizes (RSS = 712·08), model 2 fitted across all but the smallest flock size (RSS = 637·78), model 3 fitted across the smallest two flock sizes only (RSS = 91·68), while model 4 fitted across all flock sizes (RSS = 65·37; Fig. 3). Applying the extra sum of square principle among the four models (Wetherill 1986), model 4 proved to be the most parsimonious model ($F_{1,22} = 8{\cdot}85$, $P < 0{\cdot}01$ when contrasting it to the second best model, model 3).

AGGREGATIVE RESPONSES IN THE FIELD

Densities P of foraging red knots within flocks in the western Wadden Sea ranged from 0·009 to 25 birds/m^2 and were related only weakly to available prey density X (Fig. 4; $n = 355$, $R^2 = 0{\cdot}009$, $P = 0{\cdot}07$ for $\log_{10}$-transformed data). With respect to model 1, the majority of flocks fed in lower prey densities X than expected (91·0%). Even worse, virtually none of the flocks fed in such low conspecific densities P at such high prey densities X as expected by model 2 (0·3%; or 0–1·4% when taking 95% CI in estimates of functional response parameter into account; Table 1). The observed large range in predator densities P over a large range of prey densities X was as expected by model 3 (99·4%; 75·5–100%) and model 4 (95·2%; 62·8–99·4%) although, in contrast to the expectations of model 3, $P > 25$/m^2 never occurred (Fig. 4).

Discussion

FUNCTIONAL AND AGGREGATIVE RESPONSES

The model in which both interference and digestion constrain $IR_{long\text{-}term}$ (model 4) best explained the functional response of the experimental red knots (Fig. 3). In particular, the models in which no digestive constraint is included (model 1 and 2), overestimated $IR_{long\text{-}term}$ at low predator densities (Fig. 3). To a lesser extent, models in which no interference is included (model 1 and 3), overestimated $IR_{long\text{-}term}$ at high predator densities (Fig. 3).

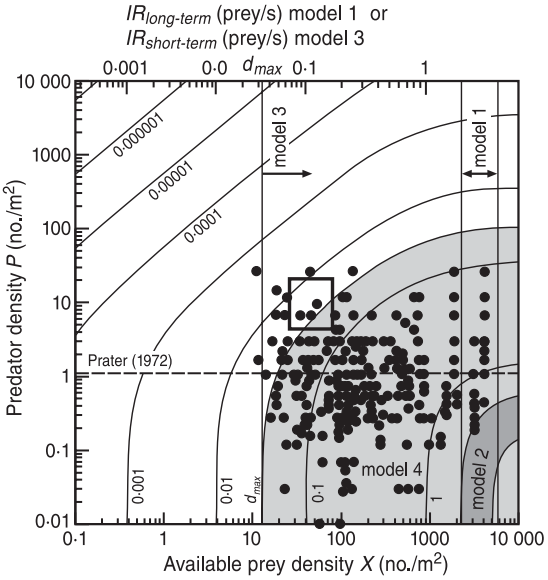

Fig. 4. Predicted and observed aggregative responses of free-living red knots (left axis) to densities X of their prey (lower axis). Model 1 predicts knots to visit only the highest prey densities, irrespective of their own density P (given by narrow vertical bar, which gives the range in maximum prey density over different years; upper axis gives predicted $IR_{long\text{-}term}$ for this model). Model 2 assumes predators do take their own density into account, and therefore predicts knots to visit only the highest prey densities at low competitor densities (given by dark grey band in the lower right corner; curved grey lines are lines of equal $IR_{long\text{-}term}$). Taking digestion into account but ignoring interference, model 3 predicts knots to visit any of those patches where $IR_{long\text{-}term}$ is constrained by maximum rate of digestion (d_{max}), irrespective of their own density (given by the right half of the graph where $IR_{long\text{-}term} = d_{max}$; upper axis gives predicted $IR_{short\text{-}term}$). Taking digestion and interference into account, model 4 predicts knots to visit any of those patches where $IR_{long\text{-}term}$ is constrained d_{max}, which is within certain lower limits on prey densities and upper, X-dependent limits on their own densities (given by large, light-grey surface where $IR_{long\text{-}term} = d_{max}$; curved grey lines are lines of equal $IR_{short\text{-}term}$). Most data on knot-densities collected in the field (n = 355) fall into the predicted regions of model 4 (95·2%) or model 3 (99·4%; although densities > 25/m^2 do not occur), while only small proportions fit the predictions of model 2 (0·3%) or model 1 (9·0%). Note that the overall mean does not differ from an estimate calculated from the mean neighbour distance between free-living, mollusc-eating red knots observed by Prater (1972; dashed horizontal line). The box in the middle of the graph indicates the ranges in P and X in the experiment.

A similar trend was observed for the aggregative responses of red knots in the field. In most flocks (99·4 and 95·2%), the birds fed in the wide range of prey and predator densities that was predicted by the models that include a digestive constraint (respectively, model 3 and 4; Fig. 4). The models in which no digestive constraint is included (models 1 and 2) predicted the knots to visit only the very highest prey densities (at the lowest predator densities in the case of model 2), which were in fact visited only by small proportions of all observed flocks (respectively, 9·0% and 0·3%). The models in which no interference is included (model 1 and 3) expected knots to also feed more densely than maximally observed (25/m^2).

Generally speaking, the costs of feeding at high competitor densities seem exaggerated by models of interference competition that do not take digestive constraints into account. Although $IR_{short\text{-}term}$ may decline with increasing predator densities, the real fitness cost would be paid only if, according to optimal foraging theory (Stephens & Krebs 1986), $IR_{long\text{-}term}$ were to decline, which it does not as long as $IR_{short\text{-}term} > d_{max}$. Maximal, 'cost-less' competitor density is reached when $IR_{short\text{-}term} = d_{max}$, and may thus become quite high for predators that need to process fair amounts of refractory material [i.e. low values of d_{max} (prey/s)], such as mollusc-eating red knots.

DIET-DEPENDENT AGGREGATIVE RESPONSES

We found additional support for the idea that digestive constraints may set maximum predator densities by looking at the composition of the diet for a number of flocks (n = 109; Fig. 5, Table 2). The best supported model (model 4) predicts the critical predator density above which $IR_{long\text{-}term}$ is affected by predator density to increase with the amount of indigestible ballast material per prey (at a given prey density X). This is because the digestive constraint equates to the amount of indigestible ballast material that can be processed internally per unit time (2·58 mg/s for birds with average gizzard sizes; van Gils *et al.* 2003a). Therefore, the upper limit to $IR_{long\text{-}term}$ due to the digestive constraint d_{max} (prey/s) will be higher when feeding on prey that contain small amounts of indigestible matter ('soft-bodied' prey) than when feeding on prey that contain large amounts of indigestible matter ('hard-shelled' prey), or formally $d_{max,\,soft\text{-}bodied} > d_{max,\,hard\text{-}shelled}$. As $IR_{long\text{-}term}$ equals maximum rate of digestion d_{max} or $IR_{short\text{-}term}$, whichever is lowest (eqn 6), predators should avoid high predator densities where $IR_{long\text{-}term}$ is not constrained by rate of digestion, because there $IR_{long\text{-}term} = IR_{short\text{-}term} < d_{max}$. Instead, they should feed at lower predator densities, where $IR_{long\text{-}term} = d_{max}$ ($< IR_{short\text{-}term}$). As $d_{max,\,soft\text{-}bodied} > d_{max,\,hard\text{-}shelled}$, the critical predator density above which $IR_{long\text{-}term}$ is affected by predator density is therefore lower when feeding on soft-bodied prey than when feeding on hard-shelled prey (Fig. 5; note that this assumes similar values for X, a, h and q for both prey types).

Diet composition was reconstructed from faecal analysis, as described by Dekinga & Piersma (1993). Indeed, we found that flocks of knots that fed on the soft-bodied crustaceans (*Carcinus maenas*, *Crangon crangon* and *Gammarus* spec.; containing on average 20 mg indigestible matter/prey, van Gils *et al.* submitted) were less densely packed than flocks that fed on hard-shelled molluscs (containing on average 78 mg indigestible matter/prey, van Gils *et al.* submitted; Fig. 5, Table 2).

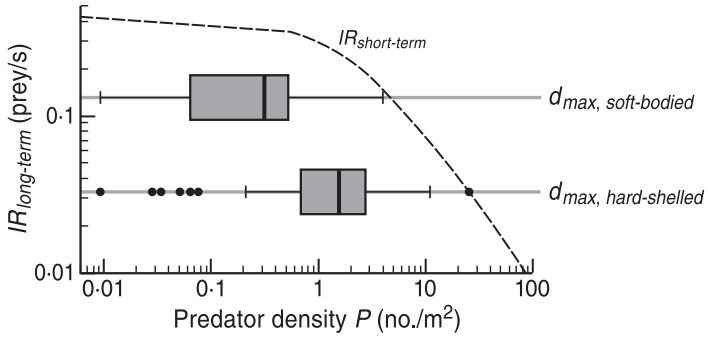

Fig. 5. Predator densities P (horizontal axis) are higher when feeding on hard-shelled prey (molluscs, lower box) than when feeding on soft-bodied prey (crustaceans, upper box; box-and-whisker plot is explained in Fig. 2). The following reasoning suggests the underlying mechanism. As soft-bodied prey items contain less indigestible ballast material, the upper limit d_{max} to long-term intake rate $IR_{long\text{-}term}$ due to the digestive constraint will be higher when feeding on soft-bodied prey than when feeding on hard-shelled prey, or formally $d_{max,\ soft\text{-}bodied} > d_{max,\ hard\text{-}shelled}$. It suffices to draw one predictive $IR_{short\text{-}term}$ that holds for both prey types (dotted line), when one assumes that both types do not differ with respect to X (212 prey/m^2 representing the mean of all occupied patches), and a, h and q as derived from the experiment. As $IR_{long\text{-}term} = \min(IR_{short\text{-}term}, d_{max})$, predators should avoid predator densities where $IR_{short\text{-}term} < d_{max}$, which is at the right of the intersection between the d_{max}-line and the $IR_{short\text{-}term}$-line. As $d_{max,\ soft\text{-}bodied} > d_{max,\ hard\text{-}shelled}$, the maximum suitable predator density is therefore lower when feeding on soft-bodied prey (~5 m^{-2}) than when feeding on hard-shelled prey (~ 25 m^{-2}).

Table 2. Analysis of variance (GLM) of the $\log_{10}$-transformed predator density in the field. Season and diet are treated as categorical variables. d.f. = degrees of freedom, SS = sum of squares, and P = significance probability. The effect of diet was a 59% reduction in predator density when feeding on soft-bodied prey compared to feeding on hard-shelled prey ($R^2 = 0{\cdot}340$)

Variable	d.f.	SS	P
Season	1	8·176	< 0·001
Diet	1	2·441	0·01
Error	106	37·544	

Two alternative explanations for this result could be proposed. First, because red knots have been shown to feed further apart with an increase in operative temperature (Wiersma & Piersma 1994) and soft-bodied prey are usually fed upon during the warmer months of the year (mainly July–August), the presence of a diet-dependent aggregative response could be driven entirely by operative temperature. To account for this effect we included the factor SEASON (either summer or fall) in the GLM, which indeed removed some significant variation (Table 2). Secondly, the assumption that interference area q is similar on both prey types may be invalid. Soft-bodied crustaceans try to run (*Carcinus*) or jump (*Crangon*) away when encountered by a red knot, in contrast to sessile hard-shelled molluscs (personal observation). To avoid neighbouring competitors kleptoparasitizing on such escaping crustaceans, red knots might maintain larger neighbour distances by more frequent and/or more intense fighting interactions, i.e. by maintaining a larger value of q. Further work is needed to disentangle this effect of q from the proposed effect of digestive constraints on diet-dependent aggregative responses.

NO COST OF INTERFERENCE COMPETITION

We suggest that red knots can live with the disadvantage of feeding in dense flocks (time loss to interference), as they already lose time through their digestive constraint. If time loss during digestive breaks accommodates fully the time lost to interference, the birds can benefit from flock life (antipredation, information) without paying the (time) cost of interference.

We propose that red knots are not the only species that 'take advantage' of their digestive constraint. We know of many examples where predators that feed on hard-to-digest prey live in dense flocks: shellfish-eating ducks (common eider *Somateria mollissima*, greater scaup *Aythya marila*, tufted duck *Aythya fuligula*), herbivorous Anatidae (swans, geese, wigeon *Anas penelope*; van Eerden 1997). Predators that feed on easy-to-digest prey live in much looser flocks; for example, the oystercatcher, being a mollusc-eating shorebird, consumes only the fleshy part and not the bulky shell material, and therefore makes a useful contrast to the red knot. As $d_{max,\ soft\text{-}bodied} > d_{max,\ hard\text{-}shelled}$ (compare Fig. 5), oystercatchers face a less stringent digestive constraint than do red knots (Kersten & Visser 1996). Although oystercatchers are about four times heavier than red knots, their densities are more than 10–100 times lower (Ens *et al*. 1996; Wanink & Zwarts 2001; Stillman *et al*. 2002b). Although the idea that aggregative responses are set partly by digestive constraints is somewhat speculative, we think it deserves further testing.

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Appendix

FUNCTIONAL RESPONSES IN DEPLETING PREY DENSITIES

In order to model $IR_{short\text{-}term}$ in depleting prey densities, we had to rewrite the short-term functional response equations (eqns 1 and 3) that are developed strictly for non-depleting cases. Assuming a single, randomly searching predator on a patch, Holling's disc equation (models 1 and 3) is rewritten to (Royama 1971; Kotler & Brown 1990; Ovadia *et al*. 2001):

$$T = Nh - \frac{\ln(1 - N/X_0)}{a} \qquad \text{eqn A1}$$

where T is the total foraging time (s) required to find and handle N prey items (i.e. $IR_{short\text{-}term} = N/T$), and X_0 is the initial prey density (no./patch). Because rate of depletion is affected by the number of predators P on a patch (even without interference), eqn A1 can be generalized to a multiple predator situation (using eqn 5 in Rita & Ranta 1998):

$$T = Nh - \frac{\ln(1 - NP/X_0)}{aP} \qquad \text{eqn A2}$$

When including interference (models 2 and 4), $IR_{short\text{-}term}$ is expected to be a proportion $(1/(1 + q(P - 1)))$ of the interference-free $IR_{short\text{-}term}$, such that eqn A2 is transformed to:

$$T = (1 + q(P - 1)) \times \left(Nh - \frac{\ln(1 - NP/X_0)}{aP} \right) \qquad \text{eqn A3}$$